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Patch exploitation by *Tribolium castaneum*: movement patterns, distribution, and oviposition

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Abstract

Stored-product insects often live in an environment of spatially separated food patches that vary considerably in size, quality, and persistence. The movement of individuals among patches of food influences the probability that stored products will become infested and pest populations will persist within storage facilities, thus affecting many aspects of pest management. We examined how a major stored-product pest, the red flour beetle, *Tribolium castaneum* (Herbst), exploits patches of food. Individuals are often inactive, periods of inactivity are often outside of food patches, males are more likely to be inactive outside of flour patches than females, and there is considerable variation among individuals in the time spent outside of patches. Beetles outside of food patches tend to be observed near edges due to a tendency to be inactive at edges, to move along edges, and to move more slowly when moving along edges. This tendency to move along edges makes beetles more likely to infest flour patches near the edges than patches further from the edge. A better understanding of the influence of landscape on pest behavior, spatial distribution, and population dynamics is needed to develop effective stored-product pest IPM programs. Published by Elsevier Science Ltd.

Keywords: Red flour beetle; Stored products; Behavior; Patch exploitation; Movement; Dispersal; Oviposition

1. Introduction

There has been considerable research into the process of insect movement (Turchin, 1998) and the function of movement when resources such as food and shelter have a patchy distribution (Hanski and Gilpin, 1997). However, studies addressing how stored-product insects interact with

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a spatially patchy landscape have been very limited. Stored-product insects live in an environment of spatially separated food patches that vary considerably in size, quality, and persistence. These food patches can be linked by insect movement among them and, at a given time, only a portion of these patches may be infested with stored-product pests. Each of these patches also has a different probability of the inhabiting insects being killed (e.g., sanitation, chemical treatment, shipment out of facility, or depletion due to feeding). Thus, the processes of emigration from, movement outside of, and colonization of food patches influence spatial distribution, probability of insect pests infesting commodities, ability of pests to persist in storage facilities, and the effectiveness of control tactics. To understand stored-product pest ecology, and ultimately to manage pest populations effectively, we need to better understand how pests interact with heterogeneous environments. The significance of food patches as refugia has been noted for some species, because of implications for the use of contact insecticides (Pinniger, 1974). Here we examined how a major stored-product pest, the red flour beetle, *Tribolium castaneum* (Herbst), exploits patches of food on a larger spatial scale than most previous studies of stored-product pests.

Tribolium castaneum is one of the major pests of processed grain and it has a high rate of movement among patches (Ziegler, 1976). Earlier studies have examined a variety of factors involved in *T. castaneum* movement within (e.g., Hagstrum and Leach, 1972; Hagstrum, 1973) and dispersal from (e.g., Ziegler, 1976; Hagstrum and Gilbert, 1976; Lavie and Ritte, 1978) patches of flour. A variety of factors can be important in the “decision” by insects to emigrate from a patch of food. Some of the factors studied include insect density (Naylor, 1961; Zyromska-Rudzka, 1966; Hagstrum and Gilbert, 1976; Ziegler, 1977), insect age (Hagstrum and Gilbert, 1976; Ziegler, 1976), and food quality (Ogden, 1970b; Ziegler, 1977). The fitness consequences of dispersal (Ziegler, 1976; Lavie and Ritte, 1978), the heritability of dispersiveness (Ogden, 1970a; Ritte and Lavie, 1977; Riddle and Dawson, 1983; Korona, 1991), and the relationship between dispersal rates and life history traits (Lavie and Ritte, 1978, 1980; Lavie, 1981; Ben-Shlomo et al., 1991) also have been investigated. *Tribolium castaneum* movement outside of, and immigration into, food patches is not as well understood. Previous studies have emphasized either only emigration from a food patch (Korona, 1991) or restricted movement between patches by using artificial channels (Naylor, 1961; Schurr and Bolduan, 1967; Lomnicki and Krawczyk, 1980; Ben-Shlomo et al., 1991). *Tribolium castaneum* responds to food volatiles (Seifelnasr et al., 1982; Phillips et al., 1993) and aggregation pheromone (Obeng-Ofori, 1991) and these may influence movement patterns and acceptance of food patches. Other internal and external factors may also influence patch use. For example, Cox et al. (1989, 1990) reported differences between strains, sexes, and ages of *Cryptolestes ferrugineus* in time spent in a refuge patch.

What has been lacking are studies of *Tribolium* behavior at larger, more realistic, spatial scales that provide multiple food patches. Studies of this type will validate and extend studies done in the laboratory and make it easier to apply results of behavior and ecology research to the management of pests in storage facilities. The objective of the current study was to investigate movement, colonization and oviposition behavior when food and shelter have a patchy distribution over an intermediate spatial scale. The two specific questions addressed in this study were (1) what are the movement patterns of red flour beetles in a patchy environment and (2) how are beetles and oviposition distributed among patches?

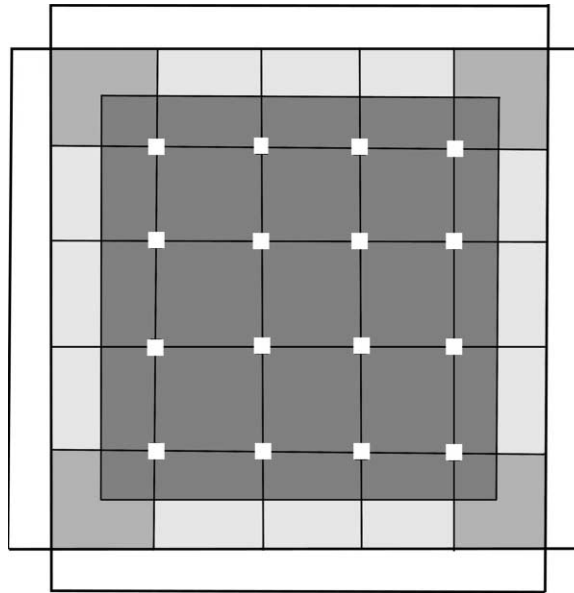


Fig. 1. A diagram of the experimental arena. The area marked with gray represents the floor ($1.2\text{ m} \times 1.2\text{ m}$) and the white sections the sides (0.3 m high) of the arena. The white squares represent the locations of the 1 g flour patches. The arena is divided into $0.24 \times 0.24\text{ m}$ zones and the zones along the edge divided in half for purposes of recording beetle locations. The dark gray parts of the arena were considered the middle region, the medium gray areas were considered the corner regions and the light gray areas were considered the sides.

2. Materials and methods

The *T. castaneum* used in this study were obtained from a laboratory colony and were used in experiments 2 weeks after emergence. To identify individual beetles, adults (males and females that were sexed as pupae) were marked with green, orange or white oil-based model paint in one to five locations (thorax and anterior or posterior half of the right and left elytra) on the dorsal surface. Depending on the experiment, either one female, one male–female pair, or 25 male–female pairs were released in the center of the arena.

The arenas used in all experiments were $1.2 \times 1.2\text{ m}^2$ plywood boxes with 0.3 m high sides and a plexiglass cover. The upper edge of the box was covered with a piece of Teflon tape to prevent insects from climbing onto the lid. Within a box, a grid of 16 evenly spaced 1 g piles of flour (i.e., patches) were placed so that the distance between the centers of two adjacent piles or an edge pile and the side of the box was 0.24 m (Fig. 1). The flour was spread to a depth of $<4\text{ mm}$ over $5 \times 5\text{ cm}^2$ pieces of black paper so they could be removed from the box easily. The arena was divided into $0.24 \times 0.24\text{ m}$ zones to record beetle positions. A series of experiments was conducted during which different parameters, such as lighting and flour patch cover, and the types of data recorded were varied. All experiments were run under ambient conditions in the laboratory under either continuous light ($>150\text{ lux}$ from a ceiling-mounted fluorescent light source) or continuous dark (arenas were only observed at the end of the experiment) conditions. The presence of beetles and eggs in patches were determined at the end of experiments. The

location of beetles outside of patches, and the paths of beetles moving outside of patches were recorded in some experiments. More details on the specific experimental protocols are described below.

2.1. Movement patterns – groups of beetles

The locations of 25 pairs of marked beetles were recorded under continuous light conditions with the patches either uncovered (two replicates) or covered with a wooden block (two replicates). Beetles were added to the arenas 16 h prior to the start of observations. The location of each of the beetles outside the piles of flour was determined every 15 min for 15 observations, with all trials started at approximately the same time of day (8:30 a.m.). The zones of the arena were combined into four areas for analysis: the flour patch regions (individuals not observed in other regions were assumed to also be in flour patches) and the middle (excluding the area occupied by the patches), corner, and side areas (Fig. 1). Differences in distribution among locations within the arena were analyzed using contingency table analysis and the chi-square (χ^2) test (Zar, 1984). Movement patterns of individual beetles were inferred using the change in location of marked individual beetles since previous observations.

2.2. Movement patterns – individual beetles

The movement patterns of individual beetles were also recorded by continuous observations of beetles over a 5 min observation period. Beetles were released into arenas 16 h prior to start of observations. Only uncovered flour patches were used and each arena contained two beetles (one male and one female). Each arena was visually inspected 15 times each day, approximately every 30 min. When a beetle was seen outside of a flour pile, it was observed for at least 5 min and its position was recorded on a map of the arena at approximately 15–30 s intervals. In some instances, observations were extended beyond the 5 min observation period and observations were terminated when beetles entered a flour pile. The arenas were each observed on four different days and new beetles were added each day (total of eight pairs). Although the same individual may have been observed multiple times, each observation was considered a separate and independent event for analysis.

The following movement parameters were calculated: speed (cm/min); proportion of observations without movement; proportion of path along the edge; and path straightness. Speed was calculated by dividing the total distance traveled by the duration of the observation. Total distance was calculated by totaling the distances between points where the beetle crossed the lines defining zones in the arena and between the start point and the first point where it crosses a line and between the last line crossed and the end point (for two observations where the individual moved, but did not cross a line the distance between start and end point was used). The proportion of observations without movement was determined based on the number of observations in which the beetle did not have any net movement during the 5 min observation period. The proportion of the path along the edge was determined by dividing the total of the path intervals near the edge (0.12 m from the edge) and along the walls of the arena by the total distance traveled. Path straightness was calculated by dividing the straight-line distance between the starting and ending points of the observation by the total path length. Due to the way that

paths were recorded, the movement parameters are only crude representations of the actual paths. However, they do provide information that is relevant to understanding beetle behavior. Data on movement parameters were analyzed using *t*-tests or Mann–Whitney tests and data on the proportion of observations with activity were analyzed using goodness-of-fit or contingency table analysis and log-likelihood ratio or χ^2 tests (Zar, 1984).

2.3. Distribution of beetles and oviposition

Depending on the experiment, either one mated female or 25 male–female pairs were released in the center of the box. The number and sex of adults and the total number of eggs laid in each pile of flour were determined after 24 h by removing the papers and sieving the beetles and eggs out of the flour. Experiments were conducted using patches of flour held either in the light or in the dark and with either glass (flour patch not shaded) or wood (flour patch shaded) covers. There were two replicates each of glass cover/dark, glass cover/light, wood cover/dark, and wood cover/light. The height of the flour in the covered patches was approximately 1–2 mm. Because of the lack of influence of cover type and light on distribution, the results of these experiments were combined for analysis unless stated otherwise. The influence of cover type on oviposition and adult retention was performed by enclosing the flour patch in a 2.5 cm square by 1 cm high cardboard box with a 3 mm diameter hole in the top. Distribution data were analyzed using ANOVA, χ^2 goodness-of-fit tests, and *t*-tests (Zar, 1984).

3. Results

3.1. Movement patterns

Observations of beetle locations with the 25 pairs of *T. castaneum* in the arenas indicated that most beetles (62% of a total of 2398 observations from both covered and uncovered treatments) were not observable at a given point in time, presumably inside flour patches, and of those beetles observed outside of patches, more individuals were located along the edges (691 observations) than in the middle (143 observations) (Fig. 2). After correcting for differences in surface area, (the total surface area of the edge regions (5184 cm²) is less than the middle region (8816 cm²), the total number of observations was greater along the edge (0.133 beetles/cm²) than in the middle (0.016 beetles/cm²). The greatest density of beetles was in the flour patches (3.715 beetles/cm²). The distribution of beetles among the regions (edge, middle, flour patches) was significantly different from the distribution expected if the beetles were distributed in proportion to the area of each region (χ^2 goodness-of-fit test; $\chi^2 = 29812$; df = 2; $P < 0.001$). Beetles were occasionally observed on the walls of the arena (78 observations or 3.2% of the total observations) and these observations were not included in the above analysis. The density of beetle observations on the walls was 0.005 beetles/cm².

Beetles observed outside food patches were more likely to be found in the 0.12 m wide section along the edge of the arena and individuals along the edge were more likely to be found in the corner (391 observations) than in the side (300 observations) regions, even though the side region (3456 cm²) had twice the surface area of the corner (1728 cm²). Correcting for differences in

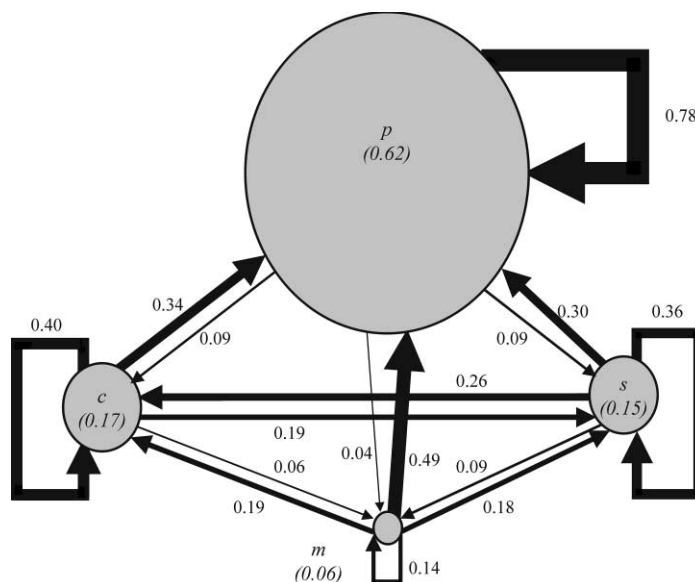


Fig. 2. An ethogram of beetle locations and transitions in an arena with x patches of flour. Circles represent the four regions of the arena: p =patch of flour; c =corner region; m =middle region; and s =side region. The proportion of observations in those locations are indicated by the number in brackets next to the letter and the diameter of the circles corresponds to the proportion of observations when beetles were in those locations. The arrows indicate transitions from one location to another. The number next to each arrow indicates the proportion of the transitions and the width of the arrow also corresponds to the proportion of transitions. All the arrows from a region total up to 1.

surface area, the total number of observations was greater in the corners (0.226 beetles/cm²) than along the sides (0.087 beetles/cm²). The difference in beetle distribution among the side, corner, and middle regions was significantly different from the distribution predicted if the beetles were distributed in proportion to the area of each region (χ^2 goodness-of-fit test; $\chi^2 = 1163$; $df = 2$; $P < 0.001$). Of the 78 beetle observations on the walls, 22 were on the walls in the corner region (0.004 beetles/cm²) and 56 were on the walls along the side region (0.006 beetles/cm²).

The location of beetles in sequential observations (15 min intervals) provides a measure of the probability of beetles moving within or between regions (Fig. 2). A total of 2240 transitions were included in the analysis, including 553 transitions that did not involve flour patches. The strongest transition trend was for beetles to enter or remain in flour patches. Beetles remained in flour patches from one observation to the next 78% of the time, but it was not determined whether they remained in the same flour patch. The trend to move into patches was strongest in beetles first observed in the middle region. Transitions among edge and corner regions occurred with approximately equal probability, but transitions from near the wall to the center occurred at much lower rates. Beetles observed in a particular corner section had a higher probability of remaining in the same section in the subsequent observation (0.38) than beetles along a side (0.17) or in the middle section (0.11). These results suggest that the tendency to be found along the edges may result from a greater tendency to move between side and corner regions and to remain in corner sections after entering. Beetles tended to move in the vicinity of the intersection of the wall and the floor, but not exclusively at the intersection.

There was a significant difference between treatments with flour patches covered with a wooden block (block) and those without a cover (no block) in the distribution of insects (2×4 contingency table and log-likelihood ratio analysis; $G = 53.1$; $df = 3$; $P < 0.001$). This difference was due to a tendency to have more beetles in flour patches and fewer beetles in the corner regions in treatments with blocks than without (2×2 contingency table and log-likelihood ratio analysis; $G = 52.8$; $df = 1$; $P < 0.001$). The proportion of observations in the side, corner, middle, or flour patch were 0.15, 0.22, 0.06, and 0.57 for without block ($n = 1050$) and 0.15, 0.11, 0.06, and 0.68 for block ($n = 1348$) treatments. This finding suggests that patch structure influences the number of beetles present. The mechanism for this is unclear, but the cover could reduce the surface area available for emigration and thus increase retention or the cover may be a visual cue and attract more beetles and thus increase immigration.

There were significant interactions among the variables sex, patch cover, and beetle distribution in arena ($2 \times 2 \times 4$ three-dimensional contingency table and χ^2 test; $\chi^2 = 72.3$; $df = 10$; $P < 0.001$) and further tests determined that there was no partial independence among the three variables. There was a significant difference in distribution between males and females in arenas with blocks (2×4 contingency table and log-likelihood analysis; $G = 11.545$; $df = 3$; $P < 0.05$) but not in arenas without blocks (2×4 contingency table and log-likelihood analysis; $G = 6.28$; $df = 3$; $P > 0.05$). The difference resulted from an increase in the proportion of males found outside of flour patches with blocks (0.71 of females in flour patches compared to 0.65 of the males) and with the additional observations of males occurring primarily in the corner regions (0.14 of the males in the corner compared to 0.08 of the females) (2×2 contingency table and log-likelihood analysis; $G = 11.542$; $df = 1$; $P < 0.001$). If the individuals remaining in the flour patches were excluded from analysis, the proportion of females observed in corners was still lower than the proportion of males (0.27 of the females compared to 0.40 of the males) (2×2 contingency table and log-likelihood analysis; $G = 6.35$; $df = 1$; $P < 0.05$).

The average number of times per trial that individuals were observed outside flour patches was 5.4 ± 0.4 for the arenas with 25 pairs of adults, but there was considerable variation among individuals (Fig. 3). There was no difference between males and females in terms of times observed outside of patches (Mann–Whitney Test; $U = 3297.5$; $df = 1$; $P = 0.845$); females averaged 5.7 ± 0.5 and males averaged 5.6 ± 0.5 observations. Individuals were more likely to be observed outside of flour patches when the patches were uncovered than covered (Mann–Whitney Test; $U = 2325.5$; $df = 1$; $P = 0.003$); the average number of observations per individual was 4.6 ± 0.6 observations with blocks and 6.4 ± 0.4 observations without blocks (Fig. 3). The proportion of the individuals within an arena that were observed outside of patches was consistent over the course of the observation period (Fig. 4).

Analysis of the movement of individual insects over ≥ 5 min observation periods supported the previous results and provided some insight into the mechanisms generating spatial distribution (Table 1). As in the previous experiment, individual beetles were more likely to be first observed along the edges or on the sides of the arena (158 observations) than in the middle (18 observations). The tendency to be observed along edges appears to result from at least three factors; (1) a tendency to be less active along edges, (2) to move at a slower speed, and (3) to move in a way that keeps the insect near the edge (Table 1). When observations were divided into those where the beetle was first observed along the edge or in the center, the insect was inactive in 82% of observations along the edge compared to 0% of the observations begun in the center. Beetles

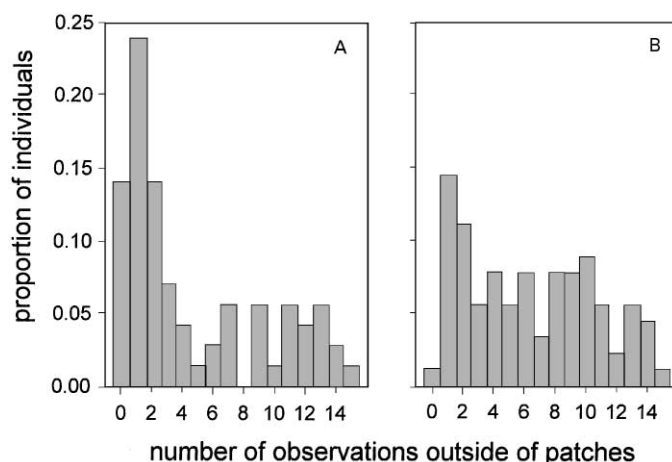


Fig. 3. The frequency distribution of the total number of times an individual was observed outside of flour patches from (A) two trials with covers on flour patches and (B) two trials without covers on flour patches. Arenas were observed 15 times during the day, between 8 a.m. and 4 p.m.

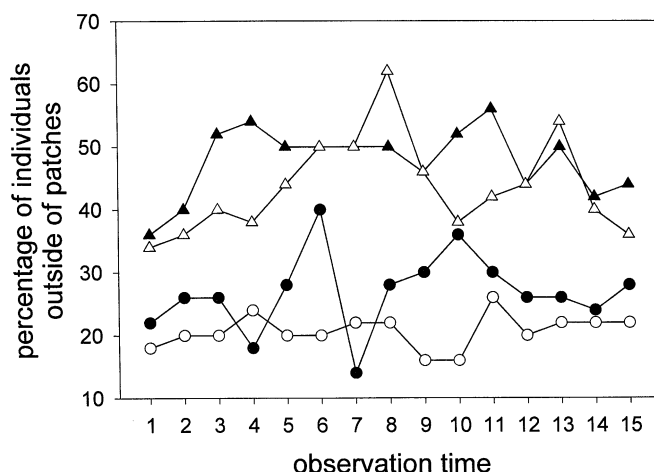


Fig. 4. Temporal variation in the percentage of beetles observed outside of flour patches in the arenas. Arenas were observed 15 times between 8 a.m. and 4 p.m. There were four replications, two block treatments (circles) that had the flour patches covered with a wood block and two no block treatments (triangles) had flour patches that were not

along the edge tended to move more slowly than beetles in the middle of the arena. The average speed of movement when a path started in the center of the arena was twice that of paths that started along the edge (Mann–Whitney Test, $U=364.7$, $df=1$; $P<0.05$) and even when the analysis only included individuals that had some net displacement, speed was still greater for beetles first observed in the center compared to the edge (Table 1). The majority of an individual's movement path during an observation period was in the edge sections, even when the beetles were first observed in the center. Paths along the edge also tended to be more linear than those in the center (Mann–Whitney Test, $U=361$, $df=1$; $P<0.05$). Increased linearity could result from the

Table 1

The influence of sex and start location on the movement parameters of individual *Tribolium castaneum* in $1.2 \times 1.2 \text{ m}^2$ arenas

Movement parameter	Group	Mean \pm SEM	No. of observations
Speed (cm/min) — all observations	Total	3.7 ± 0.7	176
	Start — edge/corner	1.8 ± 0.4	158
	Start — center	20.1 ± 3.7	18
	Male	0.65 ± 0.3	86
	Female	4.0 ± 1.0	67
Speed (cm/min) — mobile	Total	14.2 ± 1.8	46
	Start — edge/corner	10.5 ± 1.6	28
	Start — center	20.1 ± 3.7	18
	Male	6.0 ± 1.2	8
	Female	6.0 ± 0.9	19
Proportion without movement	Total	0.74	176
	Start — edge/corner	0.82	158
	Start — center	0	18
	Male	0.91	86
	Female	0.72	67
Proportion of path along edge	Total	0.79 ± 0.04	46
	Start — edge/corner	0.92 ± 0.03	28
	Start — center	0.60 ± 0.07	18
	Male	0.98 ± 0.02	8
	Female	0.87 ± 0.06	19
Path straightness (straight line distance/total path distance)	Total	0.59 ± 0.04	46
	Start — edge/corner	0.67 ± 0.06	28
	Start — center	0.46 ± 0.05	18
	Male	0.89 ± 0.05	8
	Female	0.57 ± 0.07	19

edge representing a cue for the orientation of the path or the edge constraining the available turning angles.

Females and males differed in their tendency to be active and the linearity of their paths (Table 1). The average speed of female movement was six times that of the males, but this was due to the greater proportion of the observations where males were inactive (0.91 compared to 0.72) (2×2 contingency table analysis; $\chi^2 = 10.8$; $\text{df} = 1$; $P < 0.05$). When only mobile individuals were considered, the two sexes had similar speeds of movement (t -test; $t = -0.007$; $\text{df} = 1$; $P = 0.99$). Male paths were also more linear than females (t -test; $t = -3.9$; $\text{df} = 1$; $P < 0.0001$).

3.2. Distribution of beetles and oviposition

The distribution of beetles in the flour patches after 24 h was relatively uniform. The average number of males per patch was 1.3 ± 0.1 , the average number of females was 1.4 ± 0.1 , and the average total number per patch was 2.7 ± 0.2 (average taken across all trials, $n = 8$). The maximum number of individuals recovered from a patch was 12 and the minimum 0. The percentage of

patches occupied by beetles at the end of the trial was $84 \pm 3\%$. The distribution of beetles among flour patches for the eight replicates was not different from uniform (χ^2 goodness-of-fit test; $\chi^2 = 17.06$; $df = 15$; $P > 0.05$). There was also no apparent relationship between number of males occupying a patch and females occupying a patch. The average number of beetles/patch/arena was not influenced by patch cover (glass or wood) (ANOVA; $F = 0.86$; $df = 1, 4$; $P = 0.407$) or light conditions (light or dark) (ANOVA; $F = 2.38$; $df = 1, 4$; $P = 0.198$). There was no interaction between light conditions and patch cover type (ANOVA; $F = 0.38$; $df = 1, 4$; $P = 0.570$).

The distribution of eggs was more variable than the distribution of beetles. The average number of eggs per patch was 6.8 ± 0.5 . The maximum number of eggs recovered from a patch was 29 and the minimum 0. Eggs were recovered in $78 \pm 4\%$ of the patches in an arena. There was an effect of flour patch location on the number of eggs deposited; the distribution of eggs from eight replicates was significantly different from uniform (χ^2 goodness-of-fit test; $\chi^2 = 58.2$; $df = 15$; $P < 0.05$). The average number of eggs/patch/arena was not influenced by patch cover (glass or wood) (ANOVA; $F = 5.62$; $df = 1, 4$; $P = 0.077$) or light conditions (light or dark) (ANOVA; $F = 0.00$; $df = 1, 4$; $P = 1.0$). There was no interaction between light conditions and patch cover type (ANOVA; $F = 1.60$; $df = 1, 4$; $P = 0.274$).

Given the tendency of beetles outside of patches to remain along the edges, it might be expected that the patches of flour near the edges would have more beetles and eggs than patches in the center. There was a greater number of eggs per patch along the edge regions (7.4 ± 0.6) compared to those in the center region (5.0 ± 1.0) and the distribution was significantly different from that predicted if equal numbers of eggs were laid per patch in the two locations (χ^2 goodness-of-fit test; $\chi^2 = 21.1$; $df = 1$; $P < 0.001$). There was a greater number of beetles in patches along the edge regions (3.0 ± 0.2) compared to the center (1.9 ± 0.3), and the distribution was significantly different from predicted (χ^2 goodness-of-fit test; $\chi^2 = 10.2$; $df = 1$; $P < 0.005$). The greater number of eggs in edge patches resulted primarily from a tendency to have higher oviposition along one edge of the arena; excluding the patches from this one edge made the difference in number of eggs/patch between edge and center patches not significantly different from predicted (χ^2 goodness-of-fit test; $\chi^2 = 2.9$; $df = 1$; $P > 0.05$). There was a faint shadow from the overhead lights along the arena wall on this side that may have influenced beetle behavior, although the faint shadow did not come near the flour patches.

If the time spent inactive is correlated with structure, then structures that tend to retain beetles (i.e., offering limited routes of entry and exit) should have a different distribution of beetles and eggs among patches than covered patches. The cardboard box with the hole in the lid provided limited entry and exit, but there was no significant difference in the average number of beetles per patch or the number of eggs per patch compared with the glass or wood covers. The average number of beetles/patch was 2.5 ± 0.4 for the box arenas and 2.7 ± 0.1 for the covered patch arenas (one-tailed t -test; $t = -0.60$; $df = 1$; $P > 0.05$). The average number of eggs/patch was 9.6 ± 2.7 in the box arenas and 6.8 ± 0.6 in the covered arenas (one-tailed t -test; $t = 1.04$; $df = 1$; $P > 0.05$). Although the averages were similar, the distribution of eggs was shifted so that more patches had greater numbers of eggs in the box treatment. Comparing arenas where the flour patches were enclosed in boxes to arenas where the flour patch was just covered, the proportion of flour patches with no eggs was larger (0.44 compared to 0.18), the proportion of patches with few eggs ($1 \leq x \leq 10$) was less (0.12 compared to 0.55), and the proportion of patches with > 10 eggs was greater (0.44 compared to 0.27) (2×3 contingency table analysis; $\chi^2 = 14.0$; $df = 2$; $P < 0.001$).

The distribution of beetles was not different between the box and covered treatments (2×3 contingency table analysis; $\chi^2 = 3.56$; $df = 2$; $P > 0.05$).

When single-mated females were placed in the arenas for 24 h, the average number of piles showing signs of visitation (e.g., tunneling and other forms of disturbance) was 1.8 ± 0.3 (ranging from 0–3). This is probably an underestimate of the number of patches visited, since some visits may not have caused visible disturbance to the flour. The total number of eggs laid across all the patches was 4.7 ± 0.9 (ranging from 0–10). The average number of eggs deposited per visited flour patch was 3.0 ± 0.6 and ranged from 0 to 8. Three out of 15 individuals did not oviposit at all during the observation period, and two of these showed no sign of visiting a flour patch.

4. Discussion

The interaction between environmental heterogeneity and movement behavior can have important consequences for the ecology of organisms (Turchin et al., 1991; Hanski, 1998). Movement patterns of individuals in heterogeneous environments and residency time in different patches together determine spatial distribution (With and Crist, 1995) and the degree to which patches are interconnected (Wiens et al., 1997). The extent of insect movement among patches of food will also determine the probability that stored products will become infested in a storage bin, processing facility, warehouse, transport vehicle or grocery store, the persistence of populations within storage facilities, and many aspects of pest management (e.g., the interpretation of trap catches or the effectiveness of insecticides and insect resistant packaging).

Our results indicate several aspects of pest behavior that are important in understanding the process of patch use by *T. castaneum* and have significant implications for pest management. First, beetles were usually inactive and these periods of inactivity are often outside of food patches. Males were more likely to be inactive outside of flour patches than females. Second, there was considerable variation among individuals in the time spent outside of patches. Third, when outside of food patches beetles tend to be observed near edges. Several factors tended to keep beetles along edges: a tendency to be inactive at edges, to move along edges, and to move more slowly when moving along edges. Finally, beetles were more likely to infest flour patches near the edges than patches further from the edge.

The probability of encounter and acceptance of a patch is influenced by internal and external factors. *Tribolium castaneum* behavior is influenced by food odors and aggregation pheromones (Seifelnasr et al., 1982; Obeng-Ofori, 1991; Phillips et al., 1993), but in our study there was no indication that beetles were strongly attracted to patches from any appreciable distance. This may be due to food odors and aggregation pheromones operating only over very short distances and functioning more in acceptance than in long range attraction. Due to the short duration of the experiments, levels of aggregation pheromone may not have been sufficient to elicit a strong response. Individual variation in internal state may also contribute to lack of response, because individuals that are more likely to be observed outside of patches may be those with a low response to food or aggregation cues.

Individual *T. castaneum* varied considerably in the time spent outside of food patches. Time spent in a particular patch can depend on many factors, both internal (e.g., age, mated status, sex, starvation, egg load) and external (e.g., patch location, condition, size, structure, presence of other

individuals). There are negative fitness consequences to females ovipositing in patches for extended periods of time, because larvae of *T. castaneum* are predacious on eggs (Park et al., 1965, 1974). This cannibalism restricts the time that a female can optimally exploit a food patch because newly laid eggs will have a lower probability of surviving than previously laid eggs (Ziegler, 1976). In our experiment, all patches started with new flour and movement and oviposition were observed for <24 h. Under these conditions, the distribution of beetles among patches was apparently uniform. The pattern of eggs indicates that females spend limited time in an individual patch. The probability of patches being encountered and of individuals remaining in patches is likely to be influenced by factors associated with patch quality, but further investigation is needed.

Our results indicate that the distribution of males and females within patches was similar, but that males and females differed in behavior outside of patches. Males and females would be expected to have different goals in patch exploitation. Mated females are searching primarily for oviposition locations and also for food and mating opportunities. Males, in contrast, are searching primarily for females and to lesser extent food. Cox et al. (1990) found that female *C. ferrugineus* had greater refuge seeking behavior than males. Naylor (1961) reported that female *T. castaneum* disperse more uniformly than males and that male aggregation was reduced in the presence of females. That males and females may be using food patches for different purposes raises a number of interesting issues that have yet to be addressed (e.g., where does mating typically occur, what are the optimal foraging strategies for males compared to females, how do males and females locate each other).

Based on our path analysis and the locations where beetles tended to be observed, patches near the edge should be encountered more frequently than patches away from the edge and we observed this. No flour patches were placed along the edge in this study, but based on our analysis of movement we predict that flour patches along edges would be even more likely to be exploited. Because of the large number of beetles in the arena, the relatively small size of the arena, and long observation period the tendency to exploit patches near edges may be less apparent than it would be in larger scale situations. What is not clear is how attractive food patches and aggregation pheromones are at drawing beetles away from edges. Obeng-Ofori (1991) measured paths of *T. castaneum* in response to aggregation pheromones and found that the percentage of beetles moving toward the walls dropped when aggregation pheromones were present. However, further research is needed to better understand how these cues influence insect behavior on larger spatial scales and how factors such as the state of the individual influences response.

The spatial distribution of structural elements and food patches in storage landscapes will impact pest spatial distribution and movement patterns. This has implications for the effective monitoring of pest populations because the landscape around a trap may influence the probability of the trap capturing an insect and the area that it is sampling. For example, Stejskal (1995) found lower trap catches of *T. castaneum* when food and shelter were present. Our results indicate that *T. castaneum* traps placed along walls are more likely to collect a higher numbers of insects than traps placed next to poles, because of a greater tendency for beetles to be located along edges and because of a tendency for moving individuals to travel along edges. Thus, high trap catches along walls may indicate high local populations or major routes of insect movement and this may limit the ability to effectively target control efforts such as sanitation.

The ultimate goal of pest management should be to reduce the movement of stored-product pests from the surrounding environment into the stored commodity and this can be done by

targeting source populations (e.g., targeted control tactics, sanitation) and reducing the rate of emigration (e.g., control of individuals moving outside of patches, protective barriers or packaging to reduce the inter-relatedness of the patches). The relationship between insect movement and patch use patterns in storage facilities has important implications for the infestation of commodities, monitoring, and effective use of insecticides and biological control agents that have only begun to be explored. Knowledge of insect dispersal behavior will be important in developing effective IPM programs.

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